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Home Range and Movements of *Rhabdophis tigrinus* in a Mountain Habitat of Kyoto, Japan

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Abstract: We conducted a radio-tracking study on *Rhabdophis tigrinus* to assess its spatial ecology in the Ashiu Forest Research Station, Kyoto, Japan from 2009 to 2010. The study site is located in a temperate mountain area and includes forests, grasslands, a river, open riverbanks, and small brooks. We estimated the width and area of home ranges for 11 and 10 individuals, respectively. Home range size showed a large individual variation, with home range width ranging from 97 to 997 m and area ranging from 1.3 to 11.0 ha. We did not find obvious sexual differences or effects of body size on home range size. Tracked snakes tended to aggregate in riverside areas in spring, although females were sometimes found away from the river. Compared to spring, snakes in summer and fall were relatively dispersed and more likely to be located in brookside areas or places apart from water bodies. Eight individuals moved from riverside areas to brookside areas in summer. We located hibernation sites of nine individuals. Before hibernation, four individuals moved to a mountain ridge or a steep rocky slope where snakes were never found in warmer seasons, whereas the other five individuals hibernated within their warm-season home range. Neither sex nor body size seemed to be related to the occurrence of migratory movements in summer and before hibernation. Previous studies based on visual surveys have suggested bimodal seasonal activity of *R. tigrinus*, with peaks in spring and fall. However, activity of the tracked snakes in our study did not decrease in summer compared to that in spring, suggesting underestimation of summer activity in the visual survey method. Our results suggest that *R. tigrinus* migrates to use different habitats among seasons, although there is individual variation in migratory behavior.

Key words: Space use; Seasonal migration; Hibernation site; Radiotelemetry; Snakes; Colubridae

INTRODUCTION

Spatial pattern and movements of mobile

animals reflects many aspects of their ecology and has important consequences for fitness (Holt, 2003). In snakes, factors affecting movement include physiological requirements to find locations for thermoregulation (Huey et al., 1989; Whitaker and Shine, 2002, 2003). Many snake species move long distances

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between hibernacula and warm-season home ranges before and after hibernation (Gregory, 1982). Food acquisition is another important factor. Short-term aggregation and seasonal migration to areas with high prey density is known in snakes, and thus spatiotemporal distribution of prey has a strong influence on snake movement pattern (Arnold and Wassersug, 1978; Gregory et al., 1987; Madsen and Shine, 1996). Reproductive activities are also known to affect movement. For example, males of many snake species increase movements during the mating season, presumably to search for mates (Reinert and Zappalorti, 1988; Secor, 1994; Duvall and Schuett, 1997). Female snakes often travel long distance to reach oviposition sites (Parker and Brown, 1972; Madsen, 1984).

Rhabdophis tigrinus (Colubridae: Natricinae) is one of the most common snakes in Japan, being found in a variety of habitats from forests to agricultural lands (Mishima et al., 1978; Moriguchi, 1982; Fukada, 1992). Thus, *R. tigrinus* is one of the most well-known snake species in Japan. Fukada (1992) summarized data on many aspects of its natural history, such as abundance, food habits, hibernation, and growth. His study also described the seasonality of reproductive activities: Mating occurs mainly in fall (from October to November) and also in spring (from April to June); Oviposition takes place from late June to mid-August. Several studies have reported a bimodal peak in encounter rate of *R. tigrinus*, with one peak in spring and the other in fall, suggesting bimodal seasonal activity (Fukada, 1958; Moriguchi, 1982; Moriguchi and Naito, 1982; Kadowaki, 1996). Diets of *R. tigrinus* in nature have been reported in many articles, and they have shown that *R. tigrinus* mainly feeds on anurans (e.g., Uchida and Imaizumi, 1939; Moriguchi and Naito, 1982). Extensive behavioral studies have also been conducted, especially regarding prey-handling behavior (e.g., Mori, 1997, 2006) and anti-predator behavior (e.g., Mutoh, 1983; Mori et al., 1996). An early anatomical study showed that *R. tigrinus* possesses unusual structures, called

nuchal glands, under the skin surface of its neck region (Nakamura, 1935). Recent studies using chemical analyses have demonstrated its highly unusual chemical defensive system related to these glands (Hutchinson et al., 2007, 2008, 2012; Mori et al., 2012).

Despite the considerable scientific attention that has been paid to *R. tigrinus*, information on its spatial ecology is relatively scarce. Fukada (1992) showed its monthly abundance and spatial distribution in an agricultural habitat, and Moriguchi and Naito (1983) reported movement distances obtained by a mark-recapture method in a similar habitat. However, individual movement patterns and space usage have remained unexplored because snakes in those studies were not individually followed. Furthermore, no studies have been conducted in relatively undisturbed natural habitats. In the present study, we used radio-telemetry to investigate the spatial pattern and movements of free-ranging *R. tigrinus* throughout the year in a mountain habitat of Kyoto. Specifically, we attempted to estimate home range size, describe seasonal movement patterns of individual snakes in a natural habitat, and explore possible sexual differences in space usage and movement.

MATERIALS AND METHODS

Study site

This study was conducted in the Ashiu Forest Research Station of the Field Science Education and Research Center, Kyoto University (35°18'N, 135°43'E), Japan. The altitude of the study area ranges from 355 to 725 m. Air temperature of the study site is lowest in January (the average air temperature is 0°C), and highest in August (the average air temperature is 25°C). The ground is usually covered with snow from early December until late April. Maximum snow depth exceeds 2 m. The Yura River runs across the study site, and many small brooks flow into the river (Fig. 1). The study site is hilly terrain, and most areas are covered with dense forest consisting mainly of *Aesculus turbinata*, *Pterocarya rhoifolia*,

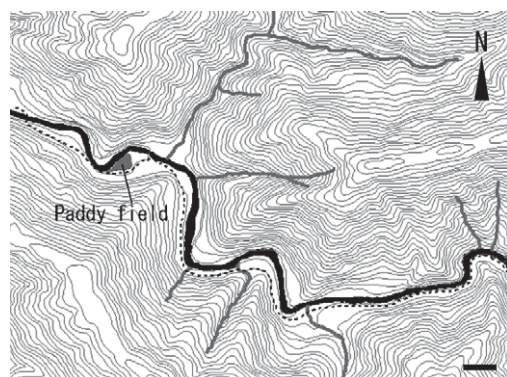


FIG. 1. Map of the study site. Black line and bold gray lines represent the Yura River (note that the river is shown in gray in the subsequent figures) and brooks, respectively. Dotted black line: trail. Narrow gray lines: contour lines at intervals of 10 m. Black bar: scale of 100 m.

Quercus cripula, *Q. salicina* and coniferous plantations (mostly *Cryptomeria japonica*). Grasslands dominated by *Miscanthus* and *Phragmites* grasses are scattered in open flat areas along the bank of the river. There is a small paddy field (ca. 0.3 ha) adjacent to the river and a small trail along the river.

Radiotelemetry

We walked through the study site mainly along the trail, the river, and the brooks in June 2009 and from May to June 2010 to collect *R. tigrinus* for radiotelemetry. We searched for snakes visually and collected them by hand. Additionally, a female (ID No. 10) and three males (ID Nos. 16, 18, and 21) were collected in April 2010 near the hibernation sites of tracked snakes (see Results). We surgically implanted radio-transmitters (Holohil, SB-2, 5 g) in 11 females and 13 males, all of which had body masses greater than 50 g (for surgical methods, see Reinert and Cundall, 1982 and Nishimura et al., 1995). All females used for radiotelemetry were gravid in the gestation season (from May to mid-July). After a three- to ten-day recovery period from surgery (average 6.8 days), the snakes were released at their initial site of capture, except for ID Nos. 1 and 5. These individuals were

mistakenly released at a point 530 m away from their original capture points. Nonetheless, they voluntarily returned to a site near their respective original capture points in 32 days.

After releasing snakes, we tried to locate each individual during the daytime approximately once a week until October. Whenever possible, the exact positions of the snakes were confirmed visually. When radio signals were coming out of a clump of vegetation, we recorded the approximate position of the snake within the vegetation. We always attempted to locate snakes at a sufficient distance to avoid disturbance. Coordinates of the locations were taken with a GPS (model 60CSx Garmin Int.). When we found a snake hiding deep under the ground in November, we terminated tracking of that individual for the year, recording that it had started to hibernate. We resumed tracking the snakes in mid-April of the following year.

Data analysis

The home range of each snake was estimated by the minimum convex polygon method. We determined width and area of home ranges for individuals that were relocated more than ten and five times, respectively. We did not estimate home range size for ID Nos. 1 and 5 (see above). Home range widths were measured on ArcMap 9 (ESRI, Redlands, CA). Home range areas were calculated using the Animal Movement extension (Hooge and Eichenlaub, 2000) for ArcGIS.

Seasons were defined as: winter (November to April), spring (May and June), summer (July and August), and fall (September and October). We estimated 50 and 95 percent utilization distributions of tracked snakes in each season using the Kernel method. The Home Range Tools extension for ArcGIS (Rodgers et al., 2007) was used for Kernel density estimation. The smoothing parameter h was calculated with the reference bandwidth method (h_{ref}) in Home Range Tools.

We defined movement distance as the distance between two consecutive locations. Movement distances were measured on ArcMap 9 (ESRI,

Redlands, CA). We excluded data from the analysis when the interval between two consecutive locations was less than 5 days or more than 15 days. We also excluded movement data of ID Nos. 1 and 5 during the first 32 days following their release (see above). There was no significant correlation between interval of locations and movement distance in the data used for this analysis (Spearman's correlation test, $r=0.13$, $P=0.22$).

RESULTS

We recorded a total of 198 locations for 24 snakes. Tracking duration ranged from 2 to 396 days (average 147 days), and the number of relocations for individual snakes ranged from 1 to 24 times (average 9.0 times). Thirteen individuals were relocated less than five times because of the death of the snake ($n=2$) or loss of radio signals. Accordingly, we estimated the width and area of home ranges for 11 and 10 individuals, respectively. The width and area of home ranges ranged from 97 to 997 m and from 1.3 to 11.0 ha, respectively. We did not find obvious effects of sex or body size on home range size (Table 1). Home ranges were largely overlapping both within and between sexes (Fig. 2). In spring, snakes predominantly used riverside areas (Fig. 3A). All 34

locations of males in spring were less than 50 m from the river. Females also mainly used riverside areas, but in six of 43 (14%) locations females were located at places more than 50 m (up to 290 m) from the river. Four tracked females were found in such habitat in spring. For example, female ID No. 3 moved from a riverside area to a brookside area in early June and moved back to the riverside area by late June (see Fig. 6A below). In summer and fall,

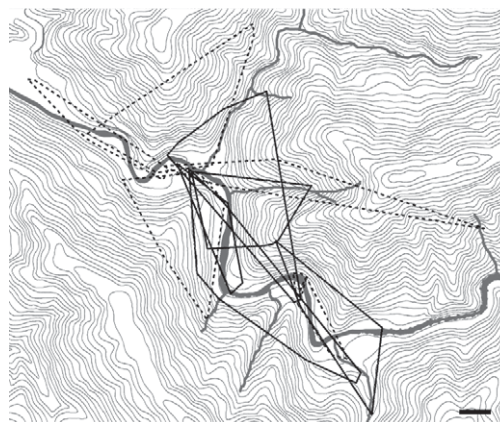


FIG. 2. Home ranges (minimum convex polygon) of 10 tracked snakes (ID Nos. 3, 4, 6, 10, 12, 13 14, 17, 18, 20). Solid and dotted polygons are home ranges of females and males, respectively. Narrow gray lines: contour lines at intervals of 10 m. Black bar: scale of 100 m.

TABLE 1. Summary data and home range of 13 *Rhabdophis tigrinus* tracked by radiotelemetry. ID: identification number. SVL: snout-vent length.

ID	Sex	SVL (mm)	Tracking period	Tracking days	Number of relocations	Home range width (m)	Home range area (ha)
3	F	702	19 Jun 2009 – 20 Jul 2010	396	18	394	6.3
4	F	745	9 Oct 2009 – 17 Jun 2010	251	13	505	2.1
5	F	750	17 Jun 2010 – 4 Nov 2010	140	12	—	—
6	F	754	19 Jun 2009 – 5 Jul 2010	381	28	923	11.0
10	F	834	29 Apr 2010 – 5 Aug 2010	98	10	637	6.0
12	M	540	24 Jun 2009 – 17 Jun 2010	358	11	607	11.0
13	M	560	23 Jun 2009 – 5 May 2010	316	13	97	2.2
14	M	591	7 Jul 2009 – 16 Sep 2009	71	10	481	2.3
16	M	622	29 Apr 2010 – 5 Aug 2010	98	7	319	—
17	M	625	5 Jun 2010 – 4 Nov 2010	152	14	532	7.7
18	M	676	29 Apr 2010 – 4 Nov 2010	189	9	290	1.3
20	M	681	5 Jun 2010 – 4 Nov 2010	152	12	997	5.9
22	M	709	29 Jul 2009 – 16 Sep 2009	49	6	372	—

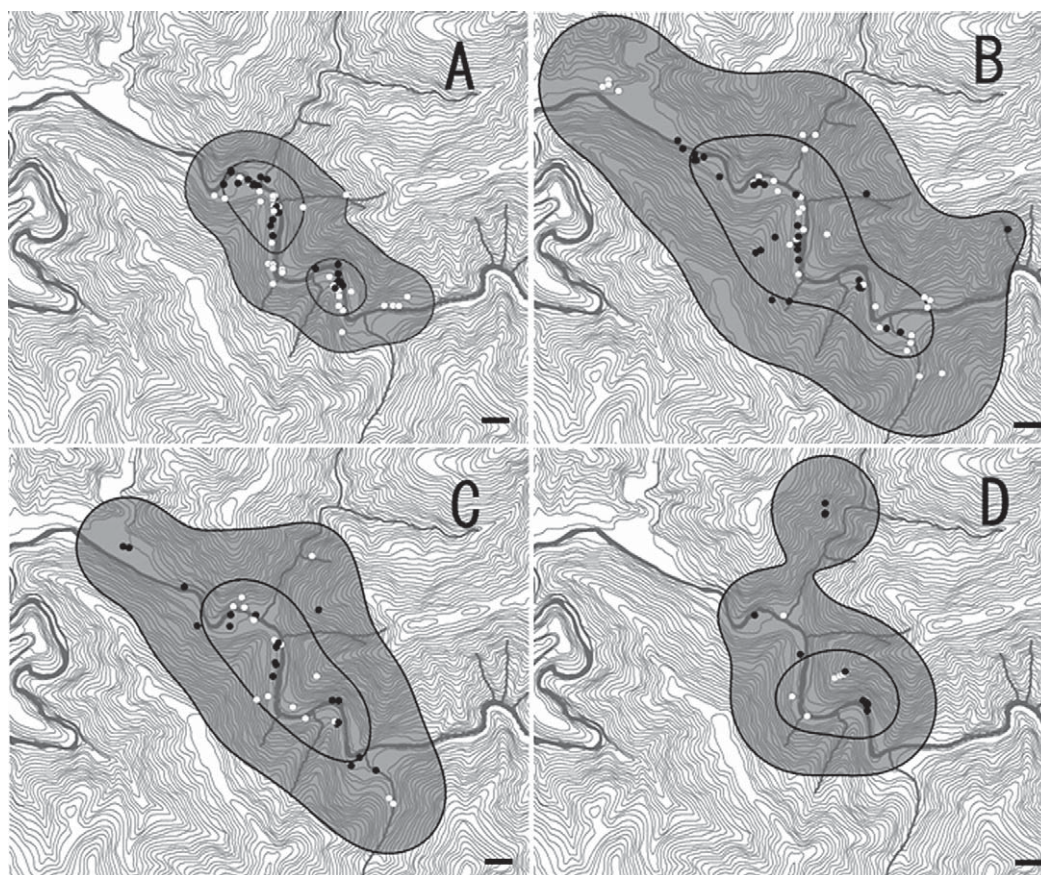


FIG. 3. Seasonal changes in distribution of tracked snakes. A) spring, B) summer, C) fall, D) winter. White and black dots represent location points of females and males, respectively. Kernel density isopleths of 95% and 50% are outlined in black, and the 95% Kernel density area is colored with gray. Narrow gray lines: contour lines at intervals of 10 m. Black bar: scale of 100 m.

both females and males still predominantly used riverside areas, but they were relatively dispersed and were more likely to be located near the brooks or in the middle of the forest away from water bodies (Fig. 3B, C). This resulted in relatively large Kernel density areas in summer and fall compared to those in spring.

Several individuals showed similar patterns of seasonal movements. Four females and four males showed long distance movements from riverside areas to brookside areas at some time between late July and August (Fig. 4). The maximum distance of these movements was 580 m. For example, ID No. 20 was located near the river from June to mid-July

and then moved 285 m to a brookside area by early August (Fig. 4D). The snakes moved vertically at most 130 m during these movements. The snakes performed these movements irrespective of sex and body size (Fig. 4).

We located the hibernation sites of nine individuals. Five (three females and two males) hibernated within the area where the snakes spent warmer seasons (Fig. 5). The remaining four individuals (one female and three males) moved before hibernation to an area where they were never found in warmer seasons (Fig. 6A, C). The maximum distance of these movements was 380 m. The snakes moved vertically at most 130 m during these movements. Neither sex nor body size seemed to be

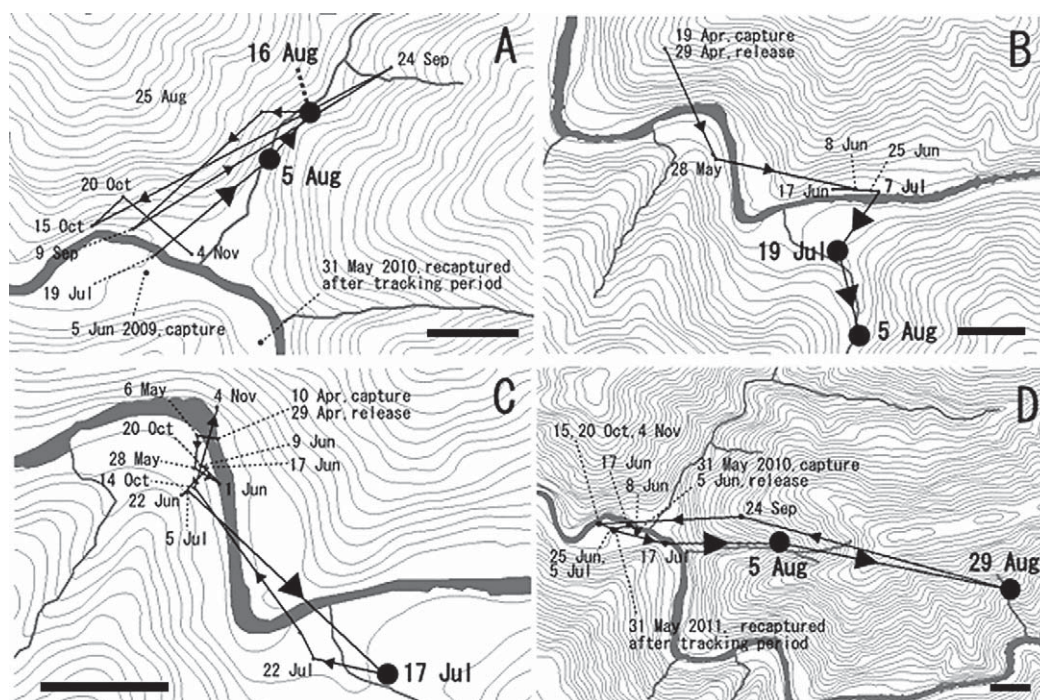


FIG. 4. Movements from riverside to brookside in summer. A) No. 5 (female), B) No. 10 (female), C) No. 18 (male), D) No. 20 (male). Dots represent location points, and large dots are location points near brooks. Consecutive location points are connected with a solid line and an arrow, and large arrows represent movement to brookside areas. Narrow gray lines: contour lines at intervals of 10 m. Black bar: scale of 100 m. ID No. 5 was released at a different point from its original capture point but moved back to the area near the capture point in 32 days (19 Jul), after which movement pattern is shown here.

related to the occurrence of these movements (Figs. 5, 6). After emerging from hibernation, three of the four snakes moved back to the area where they had spent warmer seasons in the previous year (we did not continue radio-tracking for the fourth individual). For example, ID No. 3 moved 340 m from a riverside area to a mountain ridge in mid-October and moved back to the riverside area at the beginning of the next May (Fig. 6A). The hibernation sites of the four individuals that migrated before or after hibernation were situated on a mountain ridge or a steep rocky slope rising from the river, all of which faced south. In April, we found four additional *R. tigrinus* in these hibernation sites and started radio-tracking them. They moved to riverside areas after release, showing a movement pattern similar to that of their neighbors (Fig. 6B, D).

The distributions of movement distance were right skewed in all seasons (Fig. 7). Snakes exhibited relatively short movements in spring and winter: distances moved were more than 50 m in 48% and 21% of observations in spring and winter, respectively. Long movements were relatively common in summer and fall: distance moved was more than 50 m in 69% and 76% of observations in summer and fall, respectively. Movement distance did not decrease in summer, although previous studies on *R. tigrinus* have suggested bimodal seasonal activity, with summer reduction of activity compared to that of spring and fall.

DISCUSSION

Our study presents the first radiotelemetric data on *Rhabdophis tigrinus*. These data

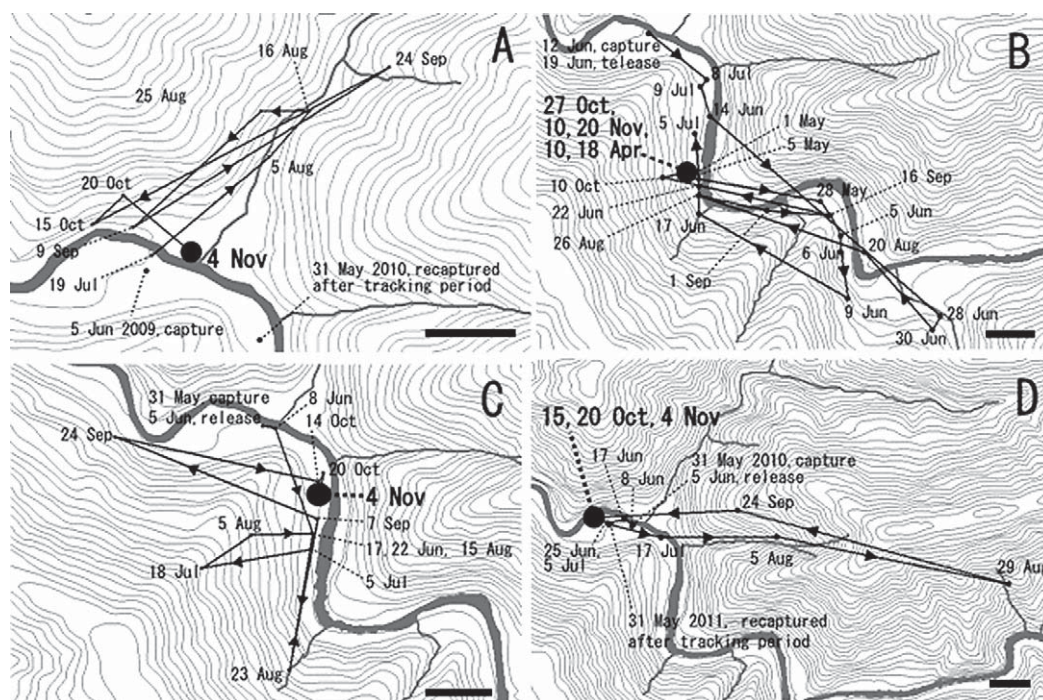


FIG. 5. Movement patterns of the tracked snakes that did not migrate before hibernation. A) No. 5 (female), B) No. 6 (female), C) No. 17 (male), D) No. 20 (male). Dots represent location points, and large dots are hibernation sites. Consecutive location points are connected with a solid line and an arrow. Narrow gray lines: contour lines with at intervals of 10 m. Black bar: scale of 100 m. ID No. 5 was released at a different point from its original capture point but moved back to the area near the capture point in 32 days (19 Jul), after which movement pattern is shown here.

showed seasonal migration of *R. tigrinus*. A common pattern exists regarding migratory movements among tracked snakes although there was individual variation in occurrence or absence of migration. Contrary to the suggestion from previous studies, our results showed unimodal seasonal activity of *R. tigrinus*, rather than bimodal. Another finding was the differences in movement pattern between gravid females and males. The following discussion refers to possible causes of observed pattern in home range, migratory movements, seasonal activity, and sexual differences in movement.

In general, home range size estimated by the minimum convex polygon method is highly dependent on the number of relocations and is largely underestimated when sample size is small (Girard et al., 2002). The sample size of

our study was not very large, so the home range sizes shown here are likely to have been underestimated. However, neither home range area nor width showed a significant correlation with the number of relocations (Spearman's correlation test, the former, $r=0.43$, $P=0.28$; the latter, $r=0.40$, $P=0.19$). The estimated home range size of *R. tigrinus* was moderate compared to that of other species of snakes (Macartney et al., 1988), although there was large variation in both the width and area of the home range in our study. The relatively large home ranges of some *R. tigrinus* were due to their long-range seasonal migrations in summer and/or for hibernation. We did not find obvious effects of sex or body size on the pattern of migratory behavior.

Several snakes in our study moved up to 380 m to and from hibernation sites. Migration

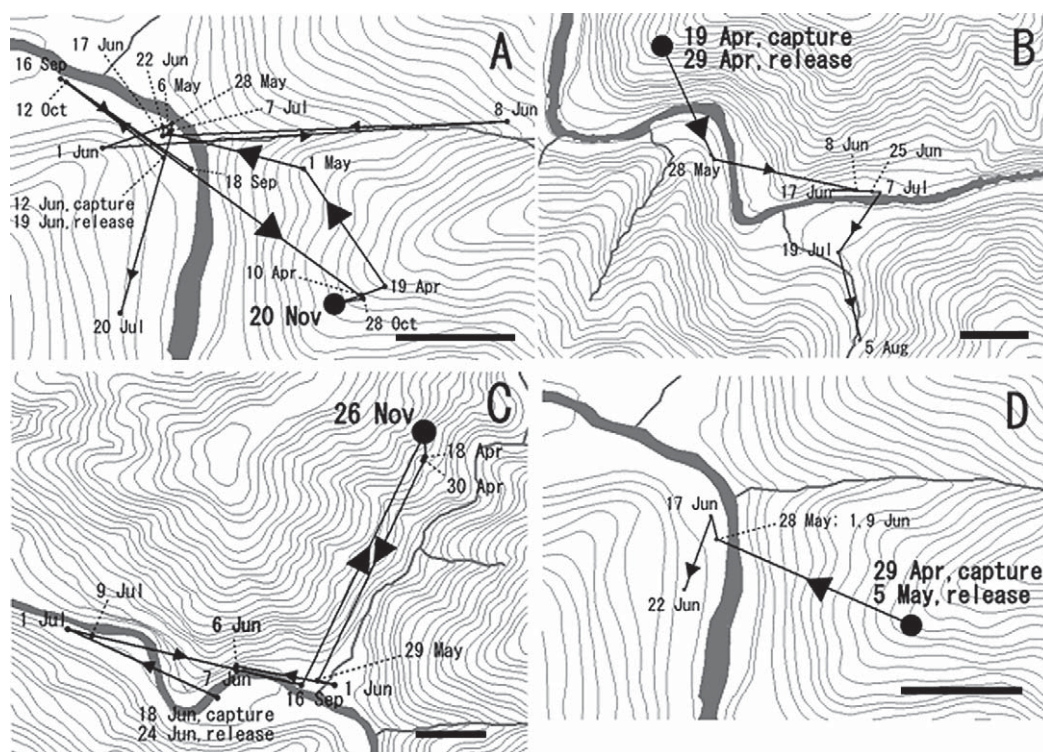


FIG. 6. Movements before and/or after hibernation. A) No. 3 (female), B) No. 10 (female), C) No. 12 (male), D) No. 16 (male). Dots represent location points, and large dots are hibernation sites. Consecutive location points are connected with a solid line and an arrow, and large arrows represent movement to hibernacula. Narrow gray lines: contour lines at intervals of 10 m. Black bar: scale of 100 m.

to and from the hibernation site is a common phenomenon among snakes in temperate regions (Gregory, 1982). The movements performed by *R. tigrinus* before and after hibernation are likely to be associated with migration between the feeding areas and appropriate hibernation sites. Fukada (1958) investigated the spatial distribution of *R. tigrinus* in flat, open agricultural landscape along a river in Kyoto. He showed that most snakes found by visual searching were distributed near the hibernacula in April and October but that snakes were scattered throughout the whole of the study area from July to September, suggesting aggregation to hibernacula and post-hibernation dispersal. Similarly, based on data obtained from mark-recapture methods, Moriguchi and Naito (1983) suggested that *R. tigrinus* in a riverside agricultural area in

Kanagawa Prefecture moves greater distances before and after hibernation compared to during warmer seasons. Migration related to hibernation might be a common phenomenon among populations of *R. tigrinus*.

The hibernation sites of the individuals that migrated before or after hibernation were situated on a mountain ridge or a steep rocky slope facing south. Southern exposure is a common feature of north-temperate hibernation sites in snakes and presumably offers thermal advantages during hibernation or spring emergence (Harvey and Weatherhead, 2006). On the mountain ridge and the steep rocky slope, we found several individuals of *R. tigrinus* other than the tracked ones in early spring. In contrast, we found no other *R. tigrinus* near the hibernation sites of the individuals that hibernated within their warm-

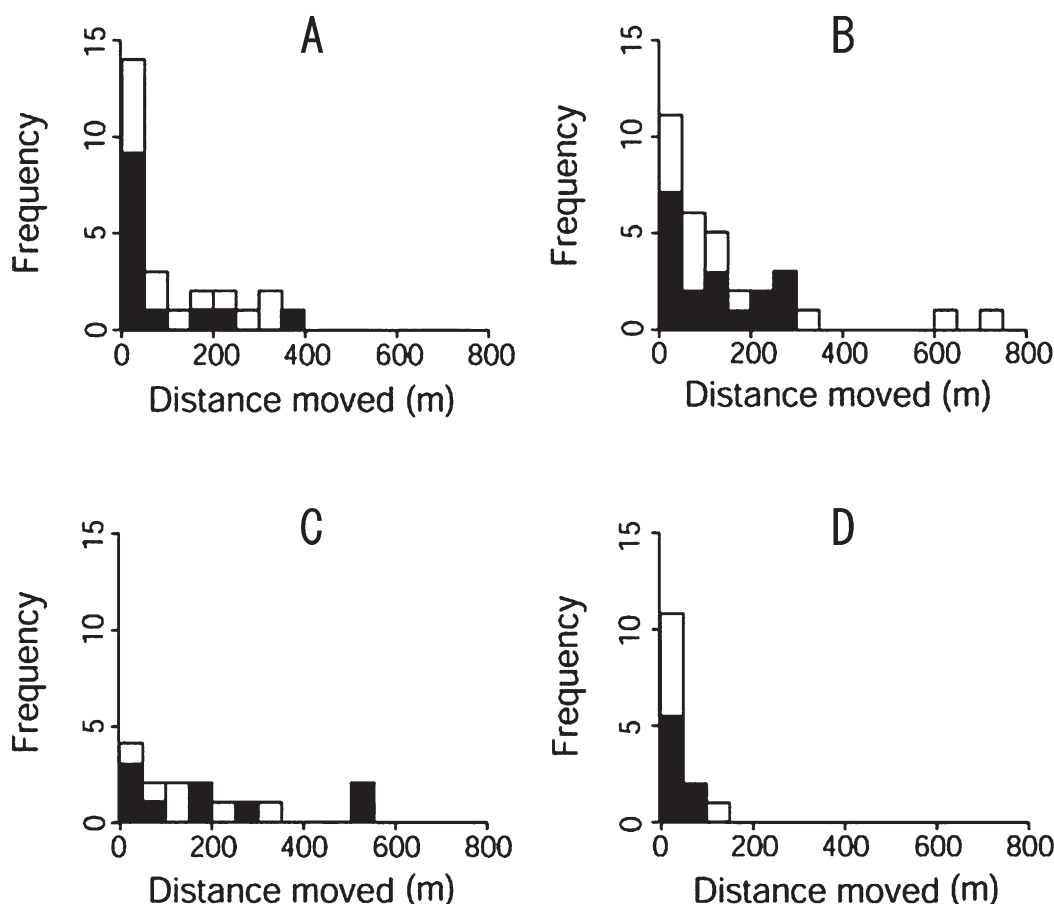


FIG. 7. Histograms of distance moved between two successive locations. A) spring, B) summer, C) fall, D) winter. Black and white parts of columns represent frequency of males and females, respectively. The interval between two successive locations was from 5 to 15 days.

season home range. Aggregation at a hibernaculum has been reported in other population of *R. tigrinus* (Fukada, 1958). These observations may suggest that *R. tigrinus* hibernates in aggregation at favorable hibernacula, like many other snakes in the northern temperate zone (Gregory, 1984; Sexton et al., 1992).

Nonetheless, some individuals hibernated within the area they used in warmer seasons. Long movements presumably incur the risk of mortality as well as energetic costs (Huey and Pianka, 1981; Gibbons and Semlitsch, 1987). Therefore, the tradeoff between the benefits of using a favorable hibernation site and the cost of migration might have resulted in variation

in migratory behavior. We do not believe that the absence of migration was the effect of implantation of the transmitter. If implantation of the transmitter affected the snake's movement, smaller snakes would be expected to be more vulnerable to it because their ratio of transmitter to body mass is larger, and they would show less tendency to migrate, which was not the case in our study.

In spring, tracked *Rhabdophis tigrinus* tended to aggregate in the riverside areas. Possible causes of this aggregation are thermoregulation and/or search for food. Open habitat offers increased solar radiation that facilitates thermoregulation, and thus snakes often prefer such habitat (Reinert, 1993;

Blouin-Demers and Weatherhead, 2001). Open habitat is limited in our study site, where terrain is hilly and most of the area is covered with dense forest. Riverside areas are open and seem to provide favorable basking sites for snakes, which might attract snakes emerging from hibernation. The main food of *R. tigrinus* at the study site is *Rhacophorus* frogs (Mori and Vincent, 2008). These frogs aggregate in the paddy field for reproduction (Kojima, personal observation), and their density around the paddy field and surrounding riverside areas remarkably increases in spring. Quantitative analyses of thermal quality and food availability are needed to verify the cause of spring aggregation to riverside areas.

In summer, tracked *R. tigrinus* moved from riverside areas to brookside areas. Fukada (1958) suggested that the spatial distribution of *R. tigrinus* is affected by food availability. Migration in response to food availability has been suggested in other snakes (e.g., Madsen and Shine, 1996). Given that food availability for *R. tigrinus* is highly seasonal (Hirai, 2004; Mori and Vincent, 2008), utilization of habitat with high food availability is one possible explanation for the summer migration. Further investigation of the relationship between food availability and snake movement pattern will be required to test this possibility.

Bimodal peaks of seasonal activity have been suggested in several studies on temperate snakes (e.g., Jackson and Franz, 1981; Gibbons and Semlitsch, 1981, 1987; Dalrymple et al., 1991; Leynaud et al., 2008). With respect to *R. tigrinus*, previous studies based on visual surveys have reported bimodal seasonal activity, with one peak in spring and the other in fall (Fukada, 1958; Moriguchi, 1982; Moriguchi and Naito, 1982; Kadowaki, 1996). However, our radio-telemetric data showed that the movement distance of *R. tigrinus* does not decrease in summer, compared to spring. Encounter rate may be affected by factors other than activity level, such as difference of observability among habitats (e.g.,

Weatherhead and Charland, 1985). In our study, the snakes in spring preferentially used open riverside areas where presumably snakes are more easily found by visual search, and in summer they used other habitats, such as dense forest, more frequently. Thus, a reduction in encounter likelihood in summer could be explained by differences in detectability between spring and summer habitats. These results imply that encounter rate by visual search is not necessarily a direct indicator of the activity level of snakes and is likely to be influenced by sampling methods (Seigel, 1986).

We did not find obvious sexual differences in either home range size or movement distance. Males of many snake species move more than females and have larger home ranges, presumably due to mate-searching behavior (Reinert and Zappalorti, 1988; Secor, 1994; Duvall and Schuett, 1997), whereas such sexual differences are not found in other snakes (Plummer, 1981; Reinert and Kodrich, 1982; Wasko and Sasa, 2009). *Rhabdophis tigrinus* may be an example of the latter type, although the number of relocations in our study may not have been sufficient to conclude that there is no sexual difference.

In several species of snakes, females have been reported to travel rapidly over long distances shortly before egg-laying to reach oviposition sites (Parker and Brown, 1972; Madsen, 1984). It has also been shown that gravid female snakes often reduce their movements during gestation and remain in a restricted area (Shine, 1979; Brown et al., 1982; Reinert and Kodrich, 1982; Gregory et al. 1987; Charland and Gregory, 1995). Our study on *R. tigrinus* showed differences in movement pattern between gravid females and males. Gravid females used both riverside areas and habitat apart from the river, in contrast to males in the same season, which remained in the riverside areas. The movements away from the river are puzzling because females appear to lay eggs in the grassland along the river (Kojima, unpublished data), and thus such movements are unlikely to be related to searching for an ovi-

position site. A detailed investigation of habitat use is required to elucidate why female *R. tigrinus* show such an unusual movement pattern during gestation.

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